A POPULATION STUDY OF THE VARIATION IN THE INFLORESCENCE OF SPIRAEA TOMENTOSA

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Introduction

In the Atlantic States and on the Coastal Plain the "common form" of *Spiraea tomentosa* L. has been described by Fernald (1912) as having a densely-flowered panicle, with the branches mostly compound, and the follicles permanently lanate. The inland phase, var. *rosea* (Raf.) Fern., has a less crowded panicle, with simple branches, and the follicles covered with tomentum which is promptly deciduous. An investigation of these characters in local population samples (Woodson, 1947) or mass collections (Anderson, 1941) and herbarium specimens corroborates the presence of two varieties. Some additional information has been obtained concerning the nature of this variation and the distribution of the two varieties.

Morphological Characters

A preliminary examination of the material assembled indicated that some of the characters used to distinguish var. *tomentosa* and var. *rosea* are of doubtful taxonomic value. In both varities the branches are simple toward the tip, but usually possess smaller branches toward the base. Whether the follicles are lanate or tomentose also does not appear to be diagnostic, and no objective method has been devised to distinguish between these two kinds of pubescence. Similarly the deciduous nature of the tomentum cannot be readily compared. In no individual plants was the tomentum entirely lacking; some persisted even on the inflorescences of the previous year. It seems that the amount of tomentum may be correlated with the age of the follicles, but no distinct tendency could be associated with either variety.

The flowers of both varieties are predominantly rose-colored, but individuals with white flowers occasionally are found. The latter condition has been described as forma *albiflora* by Macbride (1915). It may be of interest to mention that the only

white-flowered individuals observed were herbarium specimens collected within the range of var. *tomentosa*.

The present study agrees with Professor Fernald's statement that the leaves of both var. *tomentosa* and var. *rosea* vary in outline from lanceolate to ovate-oblong, and the color of the tomentum of the lower surface ranges from white to rufous. Furthermore, the outline of the inflorescence varies from ovoid to narrowly pyramidal, with the lower branches slightly spreading to strongly ascending.

The character based on the crowding or density of the flowers or fruits on the branches of the panicle appears to be paramount, for a distinction between the two varietal entities can be made in a majority of instances by visual observation. When a more objective method is used, that of counting the number of flowers or fruits along a unit length of the inflorescence, var. *rosea* again stands out as different from var. *tomentosa*. The variation of this character is the basis for this study.

Materials and Methods

Population samples, each consisting of an inflorescence bearing either mature flowers or fruits from a number of plants selected at random, were collected from 60 different localities. Individuals were picked with maximum regard to similarity of exposure on the plants, and at a sufficient distance apart to avoid clonal duplication. In most cases 25 or more individuals comprised a sample, but in a few localities a small number of plants were observed and correspondingly smaller collections were obtained.

The paucity of samples from the Middle Atlantic States, the northern Coastal Plain, and the southern and western periphery of the range necessitated some use of herbarium material. The use of this material together with population samples will be discussed later.

In each individual plant the number of flowers or fruits was determined for a unit length of one centimeter on the spire of the inflorescence, immediately above the first lateral branch. This position was selected because of its uniform exposure on the panicle, and the ease with which the flowers or fruits could be counted without destroying the structure. If the tip of the

inflorescence was damaged or destroyed, the count was made on a lower branch. A comparison of the density at the tip of the inflorescence with that of the lower branches in a large number of individuals disclosed a difference of only one flower or fruit per centimeter.

The variation in this character of crowding in local population samples is shown in Table 1, where the number of individuals are shown in the various density classes. For example, at Reedsburg, Wisconsin, the sample consisted of 63 individual plants. In 6 of these, 6 flowers or fruits were counted along one centimeter of a branch. Similarly, 13 individuals showed counts of 7, 24 had counts of 8, 14 had counts of 9, and 6 individual inflorescences were recorded as having 10 flowers or fruits per centimeter. From these data it is apparent that the range of the individuals from any one locality does not include the entire range of variability of the species-population, but varies within smaller limits about a central tendency. It may be also mentioned that the range of variation on a single plant is usually less than that of the local population. In some plants the inflorescences of the previous year persist enabling a comparison for a two year period. No significant difference in numbers was noted in this span of time.

Arithmetic means, representing the central tendencies for the samples, were computed and are also included in Table 1. Each of these values is plotted, in whole numbers, on Map 1. The plants having a tendency for densely-flowered panicles appear to predominate in the northeast portion of the range, whereas elsewhere those with less crowded inflorescences are more conspicuous.

From New Jersey to Missouri and southward only a few population samples were collected. Since the species appears to be quite rare in this region, further observations of this character were made from herbarium specimens.

A more complete coverage of the species range was made by combining herbarium specimens and population samples in the manner described by Woodson (1947). The range of *S. tomentosa* was divided into quadrats, each 100 miles square. All of the individuals collected within the limits of each quadrat were considered members of a population sample. The arithmetic means computed for these sample areas are plotted on Map 2. The results are strikingly similar to those shown in Map 1. Iso-

TABLE 1. The density of the inflorescence in population samples (mass collections) of *Spiraea tomentosa*.

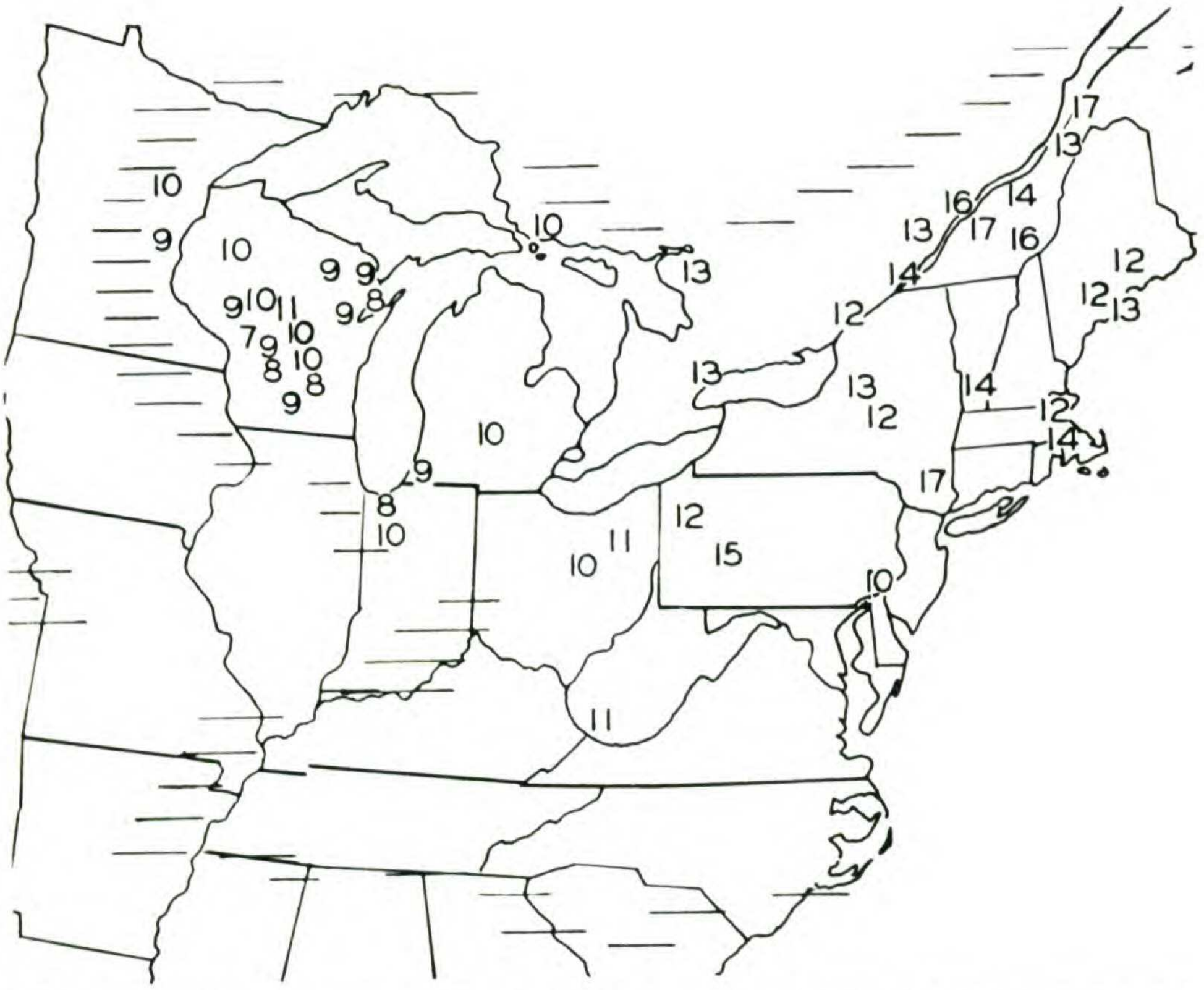
Locality	Number of flowers or fruits per centimeter																	
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	av.
WISCONSIN																		
Reedsburg	—	6	13	24	14	6	—	—	—	—	—	—	—	—	—	—	—	8.0
Hook Lake Bog	—	—	5	7	6	5	2	—	—	—	—	—	—	—	—	—	—	8.7
Millston (1)	4	11	16	9	2	—	—	—	—	—	—	—	—	—	—	—	—	6.9
Millston (2)	—	—	1	6	6	5	3	—	—	—	—	—	—	—	—	—	—	9.1
Tomah	—	2	6	7	3	2	—	—	—	—	—	—	—	—	—	—	—	7.9
Merrillan	—	—	1	11	25	20	18	1	—	—	—	—	—	—	—	—	—	9.6
Oconto	—	2	11	11	3	1	—	—	—	—	—	—	—	—	—	—	—	7.6
Sarona	—	—	—	3	9	6	2	2	—	—	—	—	—	—	—	—	—	9.6
Packwaukee	—	—	1	10	20	13	9	2	1	—	—	—	—	—	—	—	—	9.5
Mill Bluff	—	—	1	7	5	5	2	—	1	—	—	—	—	—	—	—	—	9.2
Friendship	—	—	1	9	11	13	5	1	1	—	—	—	—	—	—	—	—	9.5
Adams	—	—	—	—	4	6	1	2	—	—	—	—	—	—	—	—	—	10.1
Shawano	—	4	10	19	39	29	18	9	—	—	—	—	—	—	—	—	—	9.3
Lake Mills	—	—	—	1	3	2	1	2	1	—	—	—	—	—	—	—	—	10.3
Stanley	—	—	—	4	3	5	3	2	1	1	—	—	—	—	—	—	—	10.2
Wis. Rapids	—	—	—	7	21	16	13	10	6	1	1	—	—	—	—	—	—	10.3
Ladysmith	—	1	—	3	2	4	1	1	—	—	—	—	—	—	—	—	—	9.3
Stevens Point	—	—	—	2	4	10	9	6	3	3	—	—	—	—	—	—	—	10.9
Marinette	—	1	5	12	12	13	2	1	—	—	—	—	—	—	—	—	—	8.9
Otsego	—	—	3	5	1	1	—	—	—	—	—	—	—	—	—	—	—	8.0
Monico	1	3	4	6	5	3	1	—	—	—	—	—	—	—	—	—	—	9.0
MINNESOTA																		
Duquette	—	1	3	9	7	5	4	1	—	—	—	—	—	—	—	—	—	8.9
Nickerson	—	—	—	1	4	10	6	3	1	—	—	—	—	—	—	—	—	10.3
INDIANA																		
Enos	—	—	1	1	3	3	3	2	—	—	—	—	—	—	—	—	—	9.9
Dune Park	—	—	5	9	6	3	1	—	—	—	—	—	—	—	—	—	—	8.4
East of Gary	—	—	—	3	2	9	5	7	2	2	1	—	—	—	—	—	—	11.0

TABLE 1—(*Continued*)

Locality	Number of flowers or fruits per centimeter																	
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	av.
MICHIGAN																		
Hibbard Lake	—	—	—	5	1	3	2	—	—	—	—	—	—	—	—	—	—	9.2
Marshall	—	—	1	2	4	11	6	1	—	—	—	—	—	—	—	—	—	9.9
OHIO																		
Akron	—	—	2	5	5	6	9	4	1	1	—	1	—	—	—	—	—	10.3
Salem	—	—	—	2	2	6	3	8	1	—	2	—	—	—	—	—	—	11.1
WEST VIRGINIA																		
Clintonville	—	—	—	2	6	9	13	16	7	—	—	—	—	—	—	—	—	11.1
PENNSYLVANIA																		
Kennett	—	—	1	2	3	6	2	1	—	1	—	—	—	—	—	—	—	9.9
Harmony	—	—	—	—	3	5	11	10	9	3	2	—	—	—	—	—	—	11.8
Ingomar	—	—	—	—	—	—	1	—	4	3	4	4	1	1	2	1	—	15.3
ONTARIO																		
North Bay	—	—	1	1	6	8	1	3	—	—	—	—	—	—	—	—	—	9.8
Iron Bridge	—	—	—	5	12	15	16	12	3	2	—	—	—	—	—	—	—	10.6
Cumberland	—	—	1	2	6	9	9	9	7	1	—	—	—	—	—	—	—	10.9
Brockville	—	—	—	—	1	8	11	10	9	4	—	—	—	—	—	—	—	11.7
Huntsville	—	—	—	—	—	—	8	11	9	7	1	—	—	—	—	—	—	12.5
Hawksbury	—	—	—	1	1	7	6	11	10	12	5	3	—	—	—	—	—	12.6
Havelach	—	—	—	—	—	1	1	—	1	2	2	—	—	—	—	—	—	13.1
QUEBEC																		
Bai de Pontiac	—	—	—	1	7	12	15	11	5	1	—	—	—	—	—	—	—	11.9
Montmagny	—	—	—	—	2	3	3	1	3	6	4	2	—	2	—	—	—	13.2
St. Clotilde	—	—	—	—	1	3	5	9	17	10	8	7	3	1	—	—	—	13.5
Victoriaville	—	—	—	—	—	1	4	4	5	6	4	3	—	1	—	—	—	13.5
St. Jovite	—	—	—	—	—	2	7	10	16	14	13	8	1	1	—	—	—	13.6
Lancaster	—	—	—	—	1	—	—	2	3	3	4	2	1	—	—	—	—	13.9
Disraeli	—	—	—	—	—	—	2	5	8	10	11	10	15	10	7	2	—	15.7
Dalesville	—	—	—	—	—	—	—	—	9	12	15	14	14	7	3	1	—	15.7

TABLE 1—*Concluded*

Locality	Number of flowers or fruits per centimeter																	
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	av.
QUEBEC—(*Continued*)																		
Bon Conseil	—	—	—	—	—	—	—	1	7	7	14	19	22	16	5	4	4	16.5
Cap St. Ignace	—	—	—	—	—	—	—	—	2	11	16	19	12	13	8	6	4	16.7
MAINE																		
Norridewalk	—	—	—	—	2	2	8	13	8	2	2	—	—	—	—	—	—	12.0
Medomak	—	—	—	—	1	3	4	8	3	4	2	—	1	—	—	—	—	12.3
Boothbay Harbor	—	—	—	—	—	9	19	29	48	24	23	9	2	—	—	—	—	13.1
MASSACHUSETTS																		
Bedford	—	—	—	—	2	8	11	16	11	8	4	1	—	—	—	—	—	12.2
Lancaster	—	—	—	—	—	1	1	2	3	6	4	2	—	—	—	—	—	13.7
NEW YORK																		
Waterville	—	—	—	—	1	8	7	17	10	10	15	—	—	—	—	—	—	12.3
Malone	—	—	—	—	—	—	2	11	13	12	9	1	—	—	—	—	—	13.4
Port Jervis	—	—	—	—	—	—	—	—	—	5	8	9	15	7	4	2	—	16.6
VERMONT																		
West Dover	—	—	—	—	—	1	4	—	2	—	3	4	2	1	—	—	—	14.2



MAP. 1. Average number of flowers or fruits per centimeter in population samples of *S. tomentosa*. Lined regions represent the approximate limits of the species as plotted by Gille (1949). Not all Wisconsin localities could be included. Base map reproduction by permission of McKnight & McKnight Publishing Company.

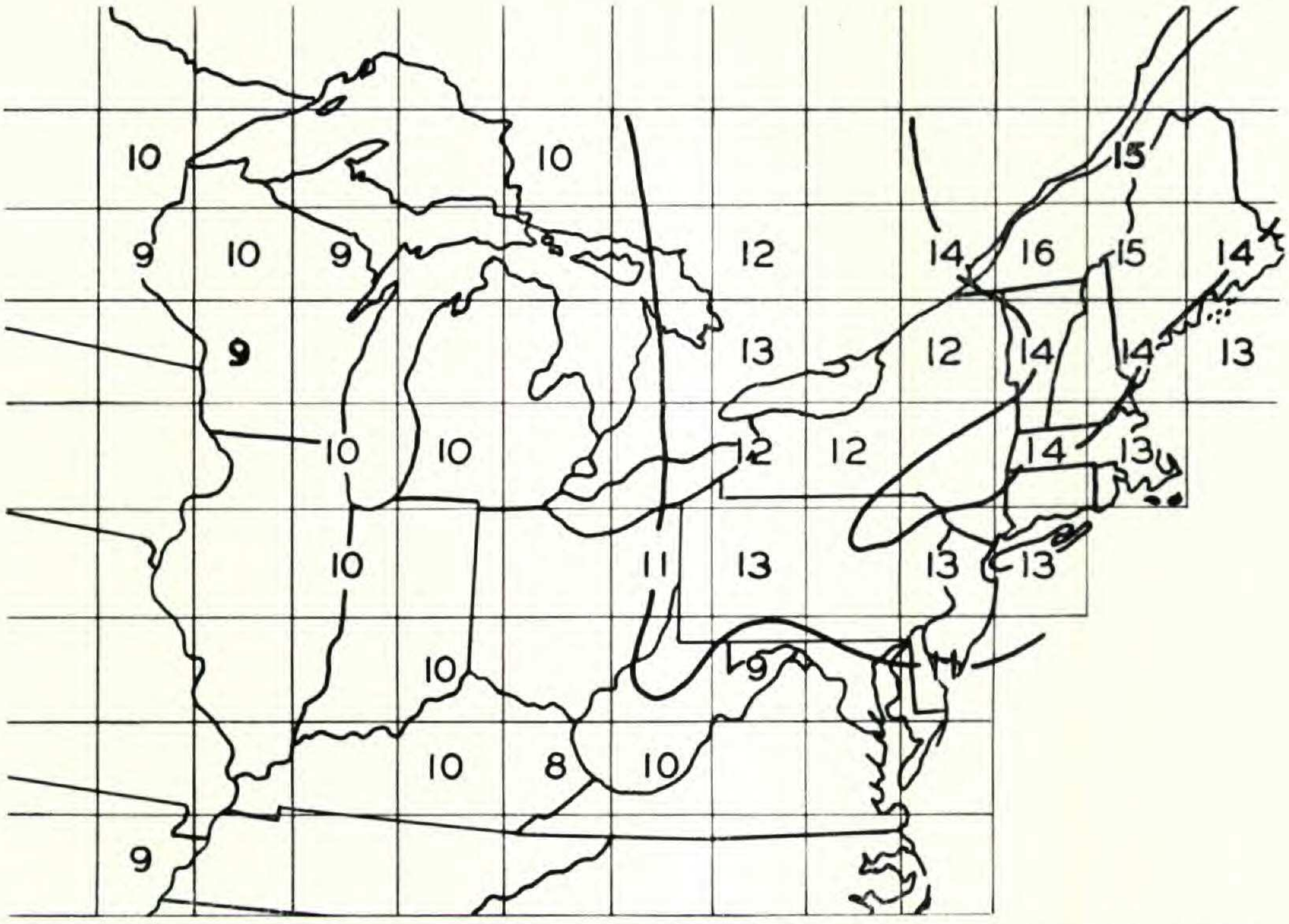
phenes of the values 11 and 14 are drawn to show the gradation of change in this character of crowding.

DISCUSSION

The pattern resulting from the two isophenes, in Map 2, is referred to as a cline. The line with the value 11 may be considered as the eastern boundary of the range of var. *rosea*, and the line with the value 14 as delimiting the western and southern boundary of extreme var. *tomentosa*. The intervening area may be considered as representing the intermediates. It is probable that this cline is the result of hybridization of individuals of the two varieites at the commissure of their ranges. Continuous back-crossing may have been responsible for the broad gradient indicated on the map. This flow of genes from one entity into another has been termed "introgressive hybridization" by

Anderson and Hubricht (1938), and shortened by other writers to "introgression."

Another interpretation of this cline may be that it represents a gradation of this character determined by environmental factors. Ecologists speak of this as an ecocline. According to



MAP. 2. Average number of flowers or fruits per centimeter in quadrat samples of *S. tomentosa*. Isophenes represent values of 11 and 14. Base map reproduction by permission of McKnight & McKnight Publishing Company.

this idea, however, it is difficult to account for a concentration of densely-flowered inflorescences only in the northeast instead of also extending into the north and northwest portions of the range where similar environmental conditions occur.

Although data are sparse from the Coastal Plain region, there is some indication that sparsely-flowered individuals predominate. Herbarium specimens collected in southern New Jersey, Delaware, and eastern Maryland are mostly of the inland phase. Fernald also noted this, but considered these plants var. *tomentosa* on the basis of the persisting lanate follicles. It was earlier pointed out that this character is of doubtful importance, therefore it seems more appropriate to consider these plants as var. *rosea*. The southward extent of this plant on the Coastal Plain

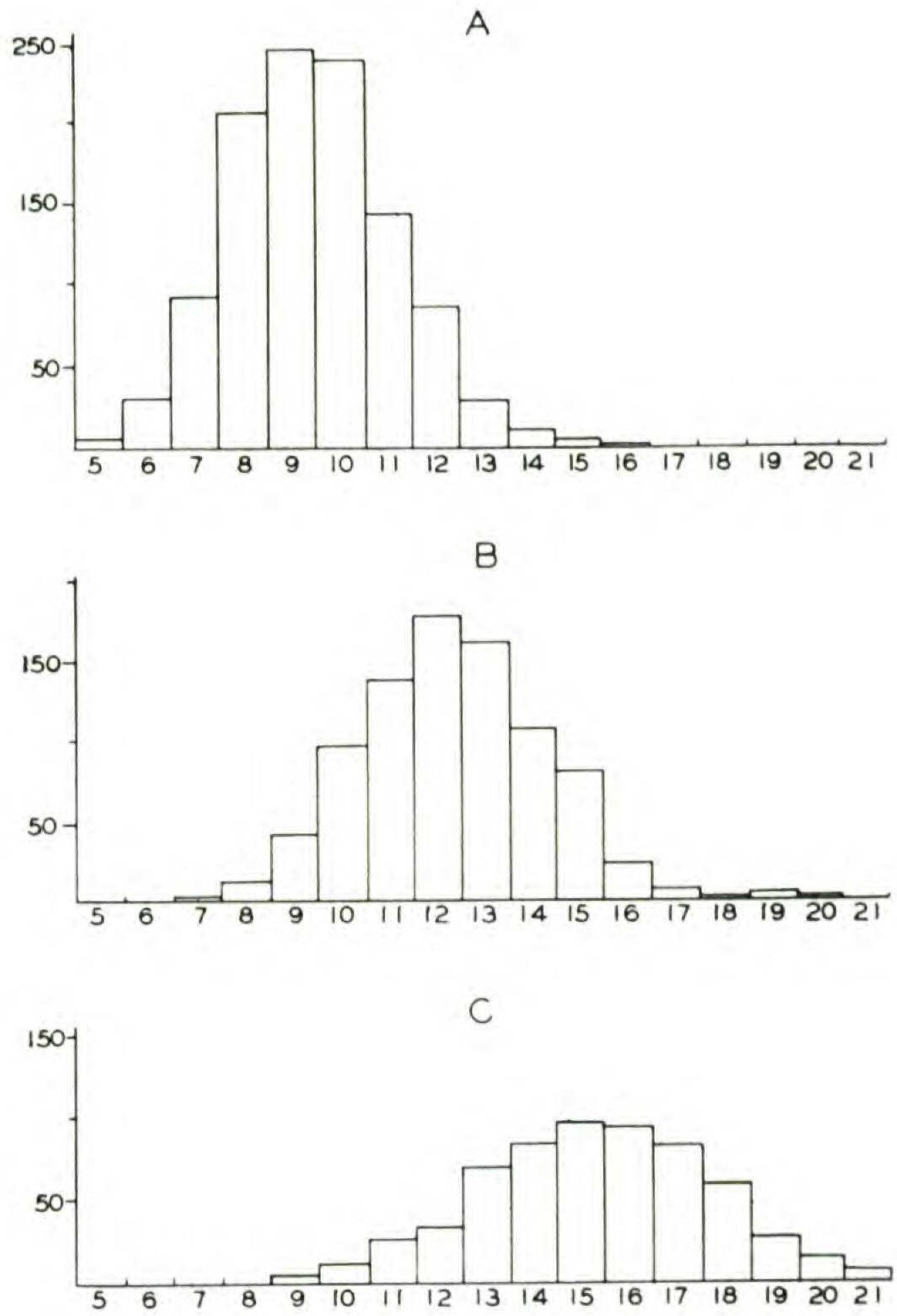


FIG. 1. Frequency distributions of individuals in population samples collected in the (A) west and south, (B) central, and (C) northeast portions of the range of the species (see Map 2). Graph (D) is a composite of (A), (B) and (C).

and the Piedmont Plateau could not be readily determined. The southeastern limit of the species, in Map 1, is based on a single specimen collected from South Carolina.[1]

In both Map 1 and Map 2 the arithmetic means along the New England coast are somewhat lower than in the interior. This suggests that some introgression of the sparsely-flowered variety may have occurred as far north as Maine and Nova Scotia.

The distribution of the individuals of population samples from the geographic area of each variety as well as of the species as a whole is shown in Fig. 1. In neither variety is the range of variation equal to that of the species. The overlapping ranges suggest a close relationship between the varieties. Individuals which may be considered var. *rosea*, in general, have 5 to 16 flowers or fruits per centimeter, while those of var. *tomentosa* generally have 9 to 21 per centimeter. This presents a problem in classifying, from the taxonomist's viewpoint, individuals within the 10 to 15 range. For example, a single specimen taken at random from a colony may have an inflorescence with a count of 10 flowers per centimeter, but the arithmetic mean for the entire colony might be 15. Is there any justification for calling this single plant var. *rosea?* Similarly it is sometimes difficult to classify population samples with intermediate averages. In general, population samples of var. *rosea* average 8 to 11 flowers or fruits per centimeter, and those of var. *tomentosa* average 14 to 17 per centimeter. Those with averages of 12 and 13 must be considered intermediates. In annotating them consideration must be given to their geographic distribution.

Although it is difficult to classify individual plants, and sometimes colonies, nevertheless, the general tendencies in the population samples show definite geographic affinities, and indicate the presence of two varieties. Since it seems necessary that some basis for distinguishing them be made, the following key will perhaps be of value.

a. Inflorescence densely-flowered, the pedicels hardly visible; in a colony the mature flowers or fruits average 12–17 per centimeter on the branches.

[1] Additional information from North Carolina has since been obtained through the courtesy of Dr. William B. Fox. Collections from Chowan, Tyrell, Bertie and Halifax counties average respectively, 9, 10, 9, and 9 flowers or fruits per centimeter.

b. Flowers rose-colored ..... *Spiraea tomentosa* L.
var. *tomentosa*
bb. Flowers white ..... *S. tomentosa* L.
var. *tomentosa*
f. *albiflora* Macbr.
aa. Inflorescence less dense than above, the pedicels easily visible; in a colony the mature flowers or fruits average 8–11 per centimeter on the branches ..... *S. tomentosa* L.
var. *rosea* (Raf.) Fern.

Ecology and Distribution

S. tomentosa ranges from Nova Scotia to Minnesota, southward to Georgia and Arkansas. Field observations in the northern portion of this range, from Wisconsin to southwestern Quebec and Pennsylvania, indicate that the species prefers open places on acid soils, especially in pastures, and at the margin of bogs, sloughs and swales. A local study of the plant in the region of Granby, Quebec (Gille, 1949) disclosed similar habitat preferences. Its presence in these habitats implies that it is a successional rather than a climax species.

Although abundant in glaciated territory, the species probably migrated from some regions south of the terminal moraine. The unglaciated Allegheny Plateau, the Ozark Plateau, and the Driftless Area of southwestern Wisconsin and adjacent portions of Illinois, Iowa and Minnesota have been considered by botanists as plant refuges. More recently Wherry (1933) considered the northern portion of the Coastal Plain and the adjacent Piedmont Plateau as another possible refuge. From these areas it is probable that the species migrated in postglacial time.

It is not known whether the two varieties of *S. tomentosa* were distinct prior to migration from these refuges. The proximity of var. *tomentosa* to the two eastern refuges seems to indicate that its route of migration was northward and northeastward from them to its present location. The distribution of var. *rosea* indicates that it may have survived in all of these areas. However, the occurrence of the plant in the Driftless Area is confined chiefly to sandy areas formerly occupied by glacial lakes. This seems to indicate a postglacial migration of the plant into the region. The sparsity of plants in the Ozarkian area may imply either a recent migration into this region or an attenuation due to increasing aridity.

These possibilities of survival and migration may account for the present distribution of the species, but fail to explain the variation in abundance throughout the range. In the northeast the species is common in open pastures. Along the southern and western peripheries of its range it is quite rare. Extensive land utilization in the latter regions may have resulted in the destruction of many habitats. It is also probable that post-glacial climatic changes may have been earlier contributing factors to this reduction in abundance. The one or more xeric periods proposed by Sears (1935) and Transeau (1935) suggest that the plants in these regions may have been reduced to relic status prior to settlement.

Summary

The study of the inflorescence of *Spiraea tomentosa*, in population samples and herbarium specimens, corroborates the presence of two varieties. The more crowded inflorescence is characteristic of var. *tomentosa*, which occurs in the northeastern part of the range of the species. Var. *rosea*, with the less crowded inflorescence, is the common phase in the interior and on the Coastal Plain. Although some individual plants of one region may seem to be characteristic of the other region, colonies within each region are quite distinct.

Acknowledgements

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FROG SPIT AND POND SCUM[1]—Marine algae are generally known as seaweeds, but there is no comparable term for the freshwater forms which include many microscopic and thread-like plants which become apparent only in great numbers and which, because of their great differences in structure and physiology, are classified in several major divisions. These small forms of life are not only curious and often beautiful, but are of interest and importance because of their place at the base of aquatic food chains and because they sometimes play a detrimental role in potable water reservoirs.

The appearance of Prescott's "Algae of the Western Great Lakes Area" marks an important milestone in Midwestern phycology. Although excluding from the present volume the diatoms and the desmids (a group in which Prescott is an authority), this *magnum opus* is still nearly a thousand pages. It represents a significant achievement of the author and an important addition to the growing list of magnificent books published at cost as a service to science by the Cranbrook Institute of Science. Although limited to aquatic algae (excluding those of the Great Lakes) of Wisconsin and Michigan, and without attention to terrestrial forms, this manual will be widely used in the United States as well as by persons especially interested in phycology throughout the world. There are recent good books in English on the morphology, physiology, and taxonomy of algae, and there is an extensive although widely scattered journal literature, but no book of regional coverage known to the reviewer describes, keys-out, and illustrates, within the limits mentioned above, all of the known algal flora of a region.

The author has worked many years, both in Wisconsin and Michigan, carrying out the survey on which his book is based and accumulating his records of about 1300 species. A very large number of published records for algae have not been accepted by Prescott. Unless substantiated by pre-

[1] *Algae of the Western Great Lakes Area*. By G. W. Prescott. xiii + 946 pp. Aug., 1951. Bull. 31, Cranbrook Institute of Science, Bloomfield Hills, Michigan. $10.50.